Do animals generally flush early and avoid the rush? A meta-analysis

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Optimal escape theory predicts that animals should balance the costs and benefits of flight. One cost of not fleeing is the ongoing cost of monitoring an approaching predator. We used a phylogenetic meta-analysis to test the general hypothesis that animals should initiate flight soon after they detect a predator—the ‘flush early and avoid the rush’ hypothesis. We found a large, significant overall relationship between the distance at which animals were approached or first detected a threat and the distance at which they fled. While these results are the first general test of the flush early and avoid the rush hypothesis, future work will be required to determine whether animals flush early to reduce ongoing attentional costs, or if they flush early as a form of risk reduction.

1. Introduction

Optimal escape theory predicts that individuals balance the costs and benefits of fleeing from predators [1–3]. Blumstein [4], recently, proposed one potential general rule in behavioural ecology which stated that animals should initiate flight soon after they detect a threat so as to reduce or to minimize ongoing attentional costs of monitoring the approaching predators. The flush early and avoid the rush hypothesis predicts that there should be a positive relationship between the predator’s starting distance (SD) or prey’s alert distance (AD) and flight initiation distance (FID). Previous support for the hypothesis came from testing the significance of correlations within a species, but these relationships are not always found [5,6]. Moreover, it is well known that statistical significance—on which such studies are based—is not synonymous with biological significance, and that there are some shortcomings of null hypothesis significance testing (e.g. lack of significance due low power; [7,8]). By contrast, estimating the effect size of a relationship gives us an estimate of the magnitude and direction of a phenomenon of interest and provides a better opportunity to understand the biological importance of a relationship [8].

Phylogenetic meta-analysis is a powerful effect size-based tool that overcomes many of the statistical limitations that may affect primary studies, beyond accounting for non-independence between species [8–10]. Hence, we conducted a phylogenetic meta-analysis to rigorously evaluate the flush early and avoid the rush hypothesis. We asked two broad questions. First, is there a uniform relationship between SD or AD and FID, and if so, what is its magnitude? Secondly, is there significant heterogeneity across taxa, and if so, what are the patterns?

2. Material and methods

(a) Data collection

To compile studies, we first searched the literature using Web of Science and Scopus for papers that cited [2] and retained those that tested the relationship between SD
(or the highly correlated AD) on FID. In sequence, we searched in the same database for studies published prior to 31 January 2012 using the terms ‘SD’, ‘AD’, ‘FID’, ‘flight distance’, ‘escape distance’, ‘approach distance’, ‘flushing distance’ and ‘response distance’. From these papers, we included studies that had variation in the SD or in the AD (rather than trying to keep it constant across trials) such that its influences on FID could be inferred. From 295 surveyed studies, 25 met the criteria.

We identified five broad taxonomic groups that have been studied: birds, mammals, lizards, snakes and arthropods. Because of insufficient sample sizes (n = 1), we excluded snakes and arthropods from phylogenetic meta-analysis (but see the electronic supplementary material, SI). Speed of predator approach is positively associated with FID [11]. Most species were originally studied with a slow approach velocity (mean ± s.e. = 34.06 ± 1.27 m min⁻¹, n = 94), but three (out of six) species of lizards were studied with a faster approach (126.5 ± 6.62 m min⁻¹, n = 3). Because of heterogeneity in approach speed, we divided lizards in two groups according to approach speed.

(b) Estimating effect sizes
We used the Pearson’s product–moment correlation coefficient, r, as our measure of effect size.

The r-value gives the strength (0, no correlation; 1, completely correlated) and direction (positive or negative) of the relationship between species FID and SD or AD. When possible, we tabulated r directly. When not provided, we used formulae in Rosenthal [12] to calculate r. If the same species was tested by two independent studies, we estimated its r as the weighted mean [13]. For five species, both SD and AD metrics were measured. In these cases, we opted to use the AD because, despite their high correlation, SD is ultimately used as a proxy for AD [2]. Studies have shown that individuals approached from distances shorter than their optimal FID flee immediately, and this can inflate the overall relationship (because r = 1 in this zone) [5,6]. To avoid incorrectly overestimating the effect size in a given species because SD was within a zone of immediate flight, we calculated effect sizes from studies that excluded data where animals flushed as soon as the experimenter moved.

(c) Phylogenetic meta-analysis
We fitted a random-model phylogenetic meta-analysis; a meta-analytic framework that explicitly accounts for non-independence of taxa through the inclusion of a covariance matrix containing phylogenetic relatedness [10]. Phylogenetic information from taxa is provided in the electronic supplementary material, SI. For analysis, r-values were transformed to Fisher’s z.

Just as in ordinary meta-analysis, the overall mean effect size was calculated as the weighted average r. Estimates were considered significant if their 95% confidence interval (CI) did not include zero [9]. We estimated I² as a measure of consistency across species [14], I² represents the proportion of observed variation that is not random error (0%, all error; 100%, no error). As part of our heterogeneity analysis, we used cluster analysis to search for homogeneous groups. To estimate publication bias [15], we used the rank correlation test [16]. Also, we calculated the fail-safe number [17], which is a metric that documents the number of unpublished studies with no effect that would be needed to eliminate an observed effect. We compared groups using z-tests. Multiple comparisons were corrected with Bonferroni correction (accepting as significant p < 0.008).

By definition, an approached animal cannot initiate the flight from a distance longer than SD or AD. This constraint can potentially create a spurious relationship between the variables if the variance increases with the distance [18]. To test the robustness of our results, we conducted a sensitivity analysis [9], where we excluded the effect sizes potentially affected by this kind of mathematical artefact (details in the electronic supplementary material, SI). We conducted the analysis with the program PHYLOMETA 1.3 [10].

3. Results
Our analysed dataset consisted of 95 species, from 23 studies, that were conducted on 5570 individuals (see the electronic supplementary material, SI). Birds and mammals approached slowly and lizards approached rapidly; all had large, positive and significant overall means (estimates ranged from 0.59 to 0.70; table 1). Pairwise comparison showed that they did not have significantly different effect sizes (table 2). Lizards
approached slowly had substantially and significantly smaller effect sizes than other groups (table 2), yet lizards approached slowly were quite homogeneous (table 1). Within other groups, there was some heterogeneity between species (table 1). An examination of dendrograms was not revealing; there was neither obvious taxonomic split nor did close relatives necessarily respond similarly (see the electronic supplementary material, S1).

With the exception of lizards approached slowly, all other groups had robust results to unpublished studies (table 1). Because effect size of lizards approached slowly differed just slightly from zero, publication of any null effect would change its effect to not different from zero. None of the taxa appeared to have publication biases (see table 1 and electronic supplementary material, S1). Finally, the sensitivity analysis showed that our results remained roughly the same after excluding effect sizes potentially estimated from a spurious relationship (see the electronic supplementary material, S1).

4. Discussion

Do animals flush early and avoid the rush? One recent study questioned the generality of the relationship by suggesting that there might be statistical problems associated with using SD as a proxy for AD [18]. However, another recent paper [19] provided a robust methodology that showed that previous conclusions using different methodologies were supported. Our meta-analysis attempted to control for some of these issues by eliminating data for individuals that flushed immediately, and permitted us to generally test the null hypothesis of no effect [6,19]. Additionally, we were careful to conduct a sensitivity analysis that excluded potential spurious relationships. The results of this additional analysis illustrate the robustness of our results. Indeed, this is the first study to explicitly evaluate and support the ‘flush early and avoid the rush’ hypothesis by demonstrating a large and positive relationship between SD (or AD) and FID. Moreover, nearly 60 per cent of the estimated effect sizes were large (i.e. r > 0.5; following Cohen [7]).

Overall, birds and mammals fled relatively soon when they detected a simulated predator (humans), despite this experimental scenario creating a low-potential risk because the person approached them slowly. By contrast, in lizards, experimental scenario creating a low-potential risk because they detected a simulated predator (humans), despite this suggested mechanism of reducing ongoing monitoring costs.

The idea that there is a cost to ongoing monitoring is based on the fact that the ability to focus attention is a limited entity, and thus must be divided among various tasks [20]. For instance, we expect that foraging success will be reduced if attention to monitoring an approaching threat is required. Thus, a prediction from our meta-analysis is that if we were to exclude those taxa with naturally low-cost monitoring, individuals from other species will flee earlier if distracted by other stimuli while being approached (e.g. sounds, multiple threats, etc.). Future studies corroborating this prediction would be consistent with the mechanism based on ongoing monitoring costs.

Based on his work with lizards, Cooper [5] suggested that individuals with relatively low monitoring costs (e.g. sit-and-wait foragers) escaped solely because of the increased risk and not owing to the attentional costs of ongoing monitoring. One possible explanation is that as the duration of a predator’s approach increases, prey may assess a greater risk. Furthermore, Cooper [5] developed a methodology that could be used (in some cases) to determine whether reduction of risk (rather than cost) is the factor influencing escape decisions. However, it is also possible that the observed relationship between FID and SD in lizards is the product of a biased sample of foraging mode or phylogenetic similarity (half of the species were phrynosomatid lizards; [6]), as well as of costs and benefits. Thus, we encourage future studies to test lizard species from other clades and with different foraging modes to clarify this issue.

Finally, our meta-analysis identified interspecific variation in flight responses within taxonomic groups, a finding that suggests that species might differentially assess increasing threats. Dendrograms and similar results between phylogenetic and ordinary meta-analysis (see the electronic supplementary material, S1) provide clues that the variation in responses between species was not accounted for by their phylogenetic relationship, suggesting a weak phylogenetic signal for this trait. Future studies that identify the traits or conditions explaining this variation would better help us understand the dynamics of risk assessment.

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References


